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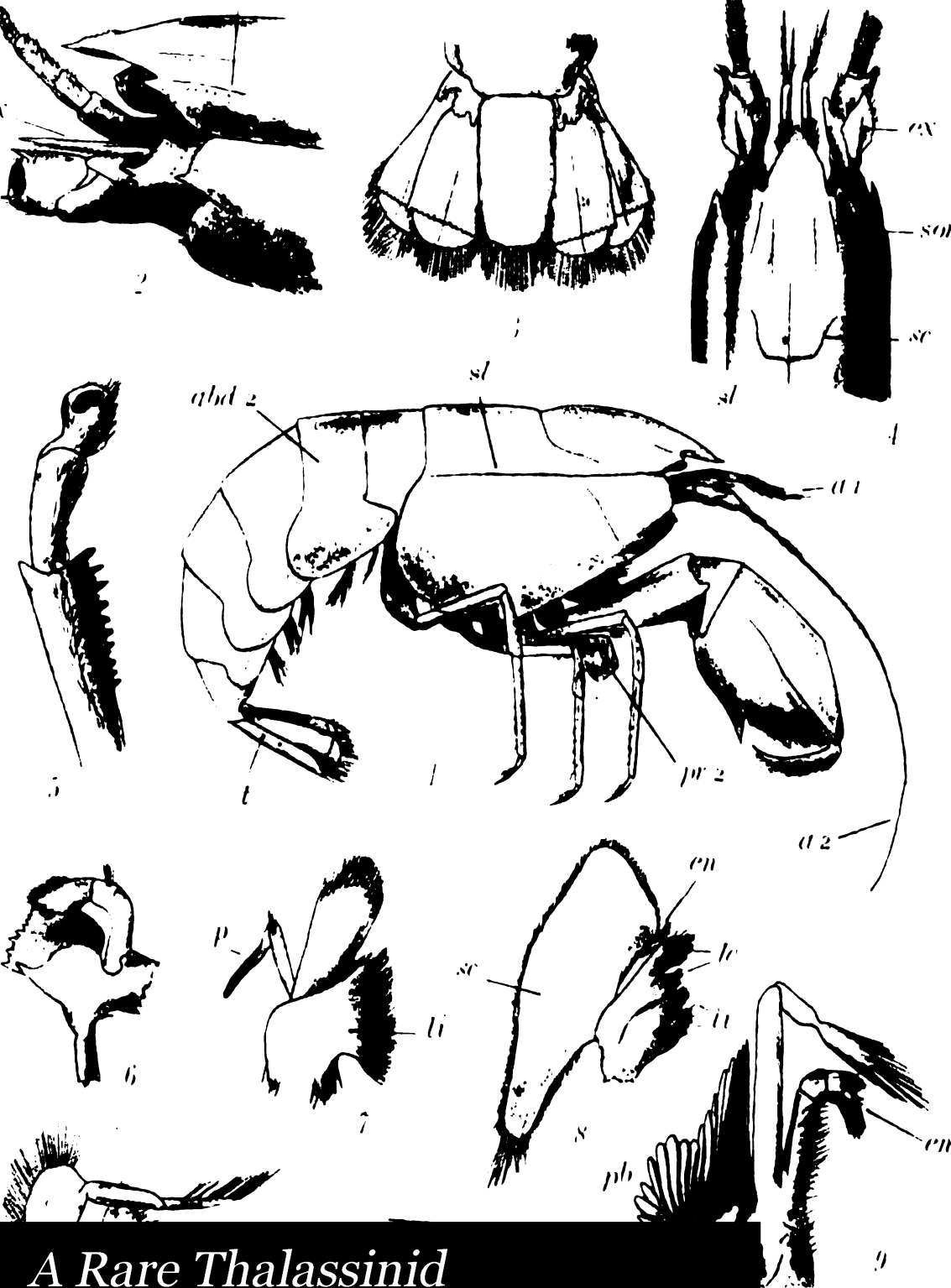
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A Rare Thalassinid and Its Larva

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A RARE THALASSINID AND ITS LARVA.

BY MILLETT T. THOMPSON.

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No. 1.— A RARE THALASSINID AND ITS LARVA.¹

BY MILLETT T. THOMPSON.

IN the summer of 1901 while working at the Woods Hole station of the United States fish commission on research that required daily examination of the plankton, my attention was attracted by a Macruran zoea which occurred at intervals throughout the latter part of August. A sufficient number of specimens was procured to permit of rearing the earlier adolescent forms. The chelipeds of these stages resembled in shape those of Crangon, Pontophilus, and other genera of the *Crangonidae*, but the structure of the zoea and mysis stages forbade reference of the larvae to any Caridian. They were, therefore, tentatively assigned to the Thalassinid, *Naushonia crangonoides*, which alone of New England Macrura, outside of the *Crangonidae*, has chelipeds of the form characteristic of that family. The correctness of this supposition was attested beyond doubt by comparison with the type specimen of *Naushonia*. Indeed, the structural resemblances were much closer than is frequently the case when adolescent and adult Decapods of the same species are compared.

So far as known, only two specimens of *Naushonia* have been collected, both of which I have had opportunity to examine. The first specimen, a male, on which Dr. J. S. Kingsley founded the genus and species, was taken by Dr. H. C. Bumpus in sand from one of the small channels on Naushon island near Woods Hole, in 1893. The other specimen, a female, was collected by Mr. G. M. Gray in July, 1899, at Ram island, a small islet in Woods Hole harbor. Mr. Gray informs me that he dug this shrimp in sand at a depth of about ten inches, the burrow having a peculiar funnel-shaped mouth. When collected it was carrying immature eggs on the abdominal appendages, but in captivity soon devoured these. The two specimens agree in all essentials and the following description applies to both except when otherwise noted, although it and the accompanying figures were prepared mainly from the type specimen.

¹ From the Anatomical laboratory, Brown university, and the laboratory of the U. S. fish commission at Woods Hole, Mass.

In the prosecution of this work on the adult and immature *Nau-
shonia*, I wish to express my especial indebtedness to Dr. H. C.
Bumpus, of the American museum of natural history, and to Mr.
G. M. Gray, collector for the Marine biological laboratory, for the
loan of specimens of the rare adult.

***Naushonia crangonoides* Kingsley.**

Length of male, 26 mm.; of female, 36 mm.

Carapace (pl. 1, figs. 1, 2, 4) cylindric, depressed in front, not
pubescent; dorsal and branchial areas sharply defined by prominent,
straight, longitudinal groove (sl) or "linea thalassinica"; dorsal
area truncate posteriorly, gastric region not much longer than car-
diac, cervical groove (sc) well marked in middle, weak at sides,
more distinct in the male; branchial areas widely rounded posteri-
orly, anteriorly with indications of a vertical groove in forward
fourth, and of a horizontal groove dividing the resulting antero-
branchial area, these grooves not visible in the female; anterior
borders of carapace finely serrate, other borders entire; external
notch well marked; antennal spine present; carapace smooth
except along grooves and ridges, and in dorsal and antero-branchial
areas, which are dotted with fine tubercles visible under a lens;
supra-orbital keel (sor) short, weak; within this another keel; an
indistinct median keel along posterior six sevenths of back; supra-
antennal spine minute; rostrum broadly triangular, flat, extending
beyond eyes; borders recurved, finely serrate, beset with fine hairs.
Epistoma free, in shape an isosceles triangle, apex serrate, borders
hairy. Sterna, where visible, flat. Genital openings indistinct, in
coxa of male, and coxal joint of female.

Abdomen (pl. 1, fig. 1) a third longer than carapace, without
carinae or spines, epimera moderate; smooth, except for microscopic
tubercles on sixth segment and telson; epimeral borders of first
and sixth segments truncate, of other segments rounded, borders
entire, with fine hairs; in female, with long hairs on inner face of
epimera near margin; dorsal borders of segments truncate; sterna
imperfectly calcified; telson (pl. 1, fig. 3) a third longer than broad,
tubercles on surface projecting backward; tip regularly rounded;
outer third of border with fringe of long hairs; no spine at external

angle. In the female the abdominal segments measure, respectively, along the back, 2, 3, 3.8, 3.9, 5, 3.3, and 4.7 millimeters.

Eyes on short peduncles, not visible from above; a minute pigment fleck.

Antennulae (pl. 1, fig. 2) with short tapering flagella; inner about half length of outer; in female shrimp, inner of about twelve, outer of fourteen joints; flagella of male broken; peduncle smooth, with fine hairs, first joint longest, distal joint not especially elongate, flattened dorso-ventrally.

Antennae (pl. 1, figs. 2, 4) with an ovate scale, whose tip reaches middle of distal joint of peduncle; surface of scale tuberculate like carapace, unequally divided by a keel; outer border serrate, both borders hairy. The peduncle consists of five subequal joints; surfaces tuberculate; apical borders of the two distal joints, toothed; flagellum present in female specimen, 24 mm. long, tapering.

Mandibles (pl. 1, fig. 6) probably subequal or equal in size, deeply excavate; borders thin, external serrate, internal with few scattered teeth; palpus two-jointed (the proximal joint may represent two fused joints), outer joint "with simple hairs on its inner, and stiff bristles on its outer margin."

First maxillae (pl. 1, fig. 7) with membranous, inflected, inner lacinia; palpus with moderate, naked flagellum, tip blunt.

Second maxillae (pl. 1, fig. 8) with narrowly divided inner and outer laciniae; endopod slender, hirsute, almost as long as inner lacinia; scaphognathite broad, membranous, produced at posterior angle and with tuft of hairs at the apex of the angle.

First maxilliped (pl. 1, fig. 10) with apex of endopod expanded, triangular, membranous, exceeding lacinia interna; peduncle calcified, cylindric; flagellum of exopod long, first joint nearly equaling outer joints taken together, peduncular joint expanded.

Second maxilliped (pl. 1, fig. 9) pediform; endopod with outer angle of penultimate joint produced; peduncle of exopod attaining tip of endopod, flagellum nearly equaling peduncle.

Third maxilliped (pl. 1, fig. 5) pediform; basal joint of endopod excavate, serrate on inner border; face of fourth joint with a series of transverse rows of short, stiff bristles (pl. 2, fig. 26); exopod attaining fourth joint of endopod.

Pereiopods with ischio-basis joint visible as in *Axius stirynchus*; without exopods; smooth; bases of first pair approximate, bases of

fifth pair nearly their own width apart, others intermediate. Chelipeds very large, subequal,—in the male specimen the left only is present,—subchelate, smooth, margins hairy; meros nearly (male) or twice (female) as long as ischium, external margins acute, teeth at inner ventral angle; carpus triangular in outline, smaller in male; propodus articulates with carpus by two tubercles, length twice (male), one and a half times (female) the breadth, margins acute; the “thumb” delimits an occludent margin half as long as the joint; acute with one large tooth and many finer teeth; dactylus bent at base at almost a right angle, arcuate, with sharp margins, the outer of which is fringed with long hairs. Second pair of pereopods (pl. 1, fig. 11) short, flattened, maxilliped-like, hairy on ventral margin; outer joints short; dactylus with long hairs. Third pair of pereopods longer than fourth or fifth, but all three pairs with long propodi and slender, arcuate dactyli.

Measurements of limbs in millimeters.

Segment.	Total length.	Ischium.	Meros.	Carpus.	Propodus.	Dactylus.
Chel. (<i>k</i>) ♂	17.8	2.5	3.1	1.2	6.5	4.5
♀	21.3	2.3	r. 4.5 l. 4.7	2.3	r. 7.0 l. 6.8	4.0
II (<i>l</i>) ♂	9.0	1.5	3.5	1.1	1.8	1.2
♀	10.5	1.0	3.7	1.5	2.0	1.3 (?)
III (<i>m</i>) ♂	12.5	2.0	4.0	1.9	3.2	1.5
♀	14.9	2.3	4.0	2.0	3.6	2.0
IV (<i>n</i>) ♂	11.0(?)	1.9	3.0	1.8	2.9	—
♀	12.5	2.0	3.0	1.7	3.4	1.4
V (<i>o</i>) ♂	10.0(?)	1.9	3.0	1.8	2.9	—
♀	—	—	3.0	2.0	3.5	1.5

Width of propodus of *k*, ♂ 3.5; ♀ r. 4.1, l. 4.4 mm.

Occludent margin of propodus of *k*, ♂ 3.8; ♀ 3.7 mm.

Gills eighteen, phyllobranch, with narrow, linear plates as in *Callianassa*; plates broader on anterior podobranchs. No pleurobranchs. Arthrobranchs, 13; the one on segment *g* small; both gills of the pairs on *h* and *i*—second and third maxillipeds—subequal; anterior gill of remaining pairs smaller than posterior. Podobranchs, 5; large on *h* and *i*; small on remaining segments. Mastigobranchs, 7; broad on *g* and *i* (pl. 1, fig. 14), slender on *h*, *k*, *l* (pl. 1, fig. 15), *m*, and *n*, weakest on *n* (pl. 1, fig. 16). A calcified

bar (cb) which is free at the tip, is attached to the base of the mastigobranchs of the pereipodal segments, *i. e.*, *k*, *l*, *m*, and *n*.

Maxillipeds.			Pereipods.					
<i>g.</i>	<i>h.</i>	<i>i.</i>	<i>k.</i>	<i>l.</i>	<i>m.</i>	<i>n.</i>	<i>o.</i>	
0	0	0	0	0	0	0	0	Pleurobranchs.
1	2	2	2	2	2	2	0	Arthrobranchs.
0	1	1	1	1	1	0	0	Podobranchs.
1	1	1	1	1	1	1	0	Mastigobranchs.

Pleopods: first pair present in female, wanting in male; uniramous, slender, tapering; one basal and several apical joints. Second to fifth pairs (pl. 1, fig. 19) biramous; rami lanceolate, subequal, hair-fringed, feebly calcified, without stylamblys. Uropods (pl. 1, fig. 13) with transverse suture on both rami; rami broad-oval, subequal, suture serrate, straight in male specimen, on inner ramus in female bent where it crosses the slight keel; borders with external spine and fringe of long hairs.

This genus clearly belongs in the Thalassinidea, but its position within that group is uncertain. The flat, prominent rostrum, well developed antennal scale, moderate abdominal epimera, and the large number of podo- and mastigobranchs recall the more primitive genera of the group, as do also the structure of the maxillae and the general form of the body. On the whole, its affinities, then, are rather with the *Axiidae* than with forms allied to *Gebia* or *Callianassa*. But in many anatomical details it differs widely from the members of this family and also, in a few cases, from all other Thalassinids. For example, the form of the carapace grooves and the phyllobranchiate gill filaments suggest *Callianassa*. The first maxilliped resembles in its general plan the appendage as developed in *Axius*, *Gebia*, *Callianassa*, and *Thalassina* (Boas, '80), but the expansion of the endopod is unlike anything found in those genera. The second maxilliped in its general form is quite unlike the corresponding appendage of the above mentioned genera, especially in the elongate angle on the penultimate joint of the endopod. *Naushonia* is further distinguished by peculiar combinations of characters. Prominent among such are the gills, which are unusually numerous (eighteen), without pleurobranchs, with noticeable development of the mastigo- and podobranchs, and with phyllobranchiate filaments;

while as a rule, phyllobranchiate filaments among the *Thalassinidea* are associated with reduction in the number of the gills, especially the ventral rows, and also pleurobranchs might be expected in a species with so large a number of gills. The internal anatomy unfortunately cannot be determined until more specimens have been collected, and we do not know whether peculiarities are present in other regions beside the exoskeleton and the appendages.

PREADOLESCENT DEVELOPMENT.

The study of the development even more than that of the anatomy tends to separate *Naushonia* from other *Thalassinids*, although it does not suggest a relationship to any remaining Crustacean group.

The zoea and mysis-stage larvae (pl. 2, fig. 20-23) resemble in habit the young of other *Macrura*. They are positively phototactic, swim on their backs with a steady motion and come to rest with the head downward, but their slender form and ruddy color render them immediately noticeable. A closer examination shows that they have a body form very unlike that of most Decapod larvae, and that this is but little altered at the successive ecdyses. Therefore the five stages of the preadolescent period may best be regarded as a unit, since zoea and mysis phases¹ cannot be satisfactorily delimited. The five stages can be differentiated as follows:—

1. Third maxilliped rudimentary. Length, 2.2-2.6 mm.
2. Third maxilliped with exopod functional as swimming organ; pereopod rudiments noticeable. Length, 4 mm. (pl. 2, fig. 20).
3. First pereopod with exopod functional as a swimming organ; remaining pereopods rudimentary. Uropods first present. Length, over 5 mm. (pl. 2, fig. 22).
4. Four anterior pereopods functional as swimming feet; rudimentary pleopods present. Length, 7-9 mm. (pl. 2, figs. 21, 24).

¹ To avoid the ambiguity caused by the use of the word "stage" to indicate not only the individual inter-ecdysal periods, but also the more comprehensive changes in form, in this paper the term will be confined to the former meaning. The more general change periods will be designated by the word "phase."

5. Fifth pereopod not rudimentary; pleopod rudiments large. Length, 9.3–10 mm. (pl. 2, fig. 23).

No specimens of these stages were collected in 1901 until the latter part of August, but last summer some first and second stages were taken as early as the middle of July. The first third stage larva was found about a week later. No fourth stage, however, was collected before the second week in August, and fifth stages not till near the end of the month. Such data indicate that the rate of development is slow, but cannot be relied upon for an accurate estimate.

The external structure and "habitus" during these stages are, as already noted, quite unusual. They have a dark brown coloration due to numerous dendritic chromatophores of that color combined with more diffused yellow pigment. The dark chromatophores cover the ventral face of the antennulae and abdomen and are more scatteringly distributed along the bases of the appendages. The yellow pigment is diffused over the eyes, antennulae, bases of appendages, rear of carapace, sides and venter of abdomen; and a single chromatophore occupies the apex of the proximal joint of the two anterior maxillipeds. The carapace is smooth, and is produced forward of the mandibles into a short "neck." The abdomen is without carinae or spines, but the outer angles of the second to the fifth segments are modified to form arcuate processes, and the angles of the telson are elongated. Arcuate processes are not developed on the sixth segment in any stage, and only imperfectly on the first segment in the earlier stages. The abdomen makes up one half of the total length in the first stage, but becomes proportionately longer in the later stages, finally being twice as long as the carapace. The free spines on the border of the telson are 10 in number in the first; 14 in the second; 14 or 15 in the third; 14 to 16 in the fourth; and 15 in the fifth stage. In the later stages one of the innermost pair is frequently much smaller than its fellow.

The mandibles (mnd) are similar in structure in all stages, but deserve especial attention because of their asymmetry. The one on the left (pl. 3, figs. 32, 34, 35) is arcuate and on the inner surface of its base are two stout teeth and within these an erect, serrate plate (pro). There is no palpus rudiment. The mandible of the right side (pl. 3, figs. 31, 33) is conical and the inner surface of the base

bears a stout process (pro) which terminates in two teeth and a serrate plate, homologous with the teeth and plate of the other mandible. A palpus rudiment (p') is present in the fifth stage. The paragnaths (p) resemble their corresponding mandibles in that they are respectively tapering and conical.

The remaining appendages are symmetrical in all stages. The eyes (pl. 2, fig. 25) are rather immobile and their shape recalls the eyes of Pagurid zoeae. The antennulae are uniramous in the first stage and on the inner surface near the apex is a long, feathered bristle. The inner ramus is developed at this point with the second stage, carrying the bristle upon its tip. This ramus becomes naked and is without joints in the later stages, and is longer than the outer ramus from the third stage on. The outer ramus becomes two- or three-jointed with the fourth, and five-jointed with the fifth stage. There are seven apical bristles in the first stage, four in the second, and two in the fourth. In the fifth stage the apex is naked. The penultimate joint in the fourth and all the proximal joints in the fifth stage bear two bristles each. The peduncular joint of the appendage becomes divided into two joints with the third stage, and into three with the fifth stage. The antennae have a narrow-oval, exopod, whose inner border bears 10, 12, 15, 13 (*circa*), 23 to 25 feathered bristles respectively in the successive stages. The endopod is cylindric; at first feather-tipped, then naked. The protopod is two-jointed from the third stage and its apical border always bears two unequal spines. The maxillae (pl. 3, fig. 34) and anterior maxillipeds call for no especial mention. The latter have a two-jointed protopod, a four-jointed endopod, and a flattened exopod tipped with six feathered bristles.

The third maxillipeds and the appendages lying posterior to them undergo more metamorphosis than the anterior appendages. These maxillipeds are uniramous and rudimentary in the first stage. The endopod appears near the base of the distal protopodal joint (pl. 2, fig. 24) with the second stage and remains rudimentary throughout the larval life. The exopod in the second and later stages resembles that of the anterior maxillipeds but is smaller. The chelipeds (*k*) are uniramous in the first and biramous in the second stage, but no trace of the chela can be found even in the fifth stage. The exopod is first functional in the third stage. The second (*l*), third (*m*), and fourth (*n*) pairs of limbs are uniramous in the first

two stages and become biramous with the third stage. The exopods are functional in the fourth stage. When functional, exopods of all the pereopods resemble those of the third maxilliped. The fifth pair of limbs (*o*) is uniramous throughout the larval period. Gills appear in the fourth stage with the rudiments of all the arthro-branches and a single common rudiment for the mastigo- and podo-branches of each segment except *l*, *m*, and *n*. These are introduced with the fifth stage (pl. 2, fig. 30). The pleopods are introduced on segments two to five with the fourth stage and remain rudimentary during the following stage. They are biramous. The uropods enter with the third stage.

Although a fairly large number of young *Naushonia* was obtained both in 1901 and in the past summer, it has not been possible to study the internal anatomy in detail owing to difficulties in technique usual to the study of Crustacea. The results that have been obtained, however, show that in most respects the anatomy does not differ from that of other Decapod larvae. The stomach is laterally compressed, much deeper than broad, with a weak dorsal tooth, lateral teeth which project upward rather horizontally, and the cardio-pyloric and median pyloric valves, (the two latter being apparently confluent in the first stage). From at least the second stage on, the lateral teeth and the median pyloric valve end posteriorly in short, slender spurs so that, with the dorsal valve, there are four pyloro-intestinal valves. The lateral teeth and median pyloric valve are setose from the second stage, but the cardio-pyloric valve remains smooth until the third stage. Lateral pyloric pouches are introduced with the second stage, and oesophageal plates with the fourth stage. The stomachal musculature is simple, consisting, as in other zoeae, of dorsal and ventral supporting muscles. The intestine shows no chitinous lining until the middle of the sixth abdominal segment is reached. The cells of this achitinous part (*int*) — presumptive midgut — are short for the greater portion of its extent, but become more columnar anteriorly. Their free borders are rounded into the lumen. The chitinous gut (*ch int*) — presumptive postgut — has moderately long, columnar cells which are more vacuolated than the cells of the achitinous gut, and at the point of union with the latter, the cells form prominent ridges, the methoria. The livers are the only diverticula from the intestine in the preadolescent stages, and the cells which make up their

walls have the characteristic granular vacuolated protoplasm and large nuclei. The lumen is ample and communicates widely with the lateral pyloric pouches of the stomach. In the first stages of development these glands are simple cylinders which extend forward beyond the oesophagus and backward into the potential thorax. The anterior and posterior ends are tapering. But in the third and later stages the region lying posterior to the stomach gives off a longitudinal series of lateral, and several dorsal diverticula.

At the time of the moult to the adolescent phase a diverticulum, the intestinal caecum, arises from the dorsal wall of the achitinous gut just caudad from the methoria, which at this period lie farther forward than in the earlier stages. This caecum has a similar development in the genus *Eupagurus*, just forward of the methoria in the fifth abdominal segment; and, in this form, caecum and methoria lie farther and farther forward in successive stages until the latter reach their adult position in the second abdominal segment and the caecum becomes thoracic. The mechanism of this change is not clear in either instance, and in *Naushonia*, of course, the definitive position of the methoria and caecum is not known. As the chitinous gut in *Gebia* and *Callianassa* is shorter than with most *Macrurus* forms, it is possible that in *Naushonia* the methoria are only barely thoracic in the adult.

Aorta, antennary, superior abdominal, and sternal arteries are present in all the stages. Hepatic arteries, however, are not developed in preadolescent life. A similar retardation in the development of the hepatic arteries is found in *Eupagurus*, and Claus ('84) figures a well advanced larva of the Adriatic *Thalassinid*, *Calliaxis*, with antennary but without hepatic vessels. It seems to be more usual among *Decapods*, however, for both pairs of arteries to be developed at the same time. The antennary arteries give off branches to the antennae, eyes, and stomach (pl. 2, fig. 23). In the mysis stages at least, and in the earlier stages, there is an enlargement of the aorta near the base of the rostrum (pl. 2, figs. 21, 25). Segmental arteries from the superior abdominal, with the exception of those for the sixth segment, are found in all stages. Those for the sixth segment are first detected in fourth-stage larvae, but they possibly arise earlier. The ventral abdominal artery is unbranched. It was not possible to determine the arrangement of the ventral thoracic artery in the different stages, beyond tracing the main trunk to the region of the head in a fourth-stage specimen.

The abdominal musculature is the same as that of an adult *Macruran*. A green gland is found in all stages, but in the first stage its lumen is limited and the cells which make up the wall resemble somewhat the undifferentiated cells which occur in all parts of the body during larval development. In the succeeding stages, however, the histology which characterizes this organ in Crustacean larvae becomes apparent; *i. e.*, the cell boundaries are indistinct, the protoplasm is homogeneous, granular, and stains darkly, and the nuclei are large with a well marked reticulum. Diverticula arise in the fourth stage. A small shell gland (pl. 3, fig. 41, sh g) is also present throughout the preadolescent period.

The *Naushonia* young have one very remarkable internal structure (pl. 3, fig. 41, vg). This is a cluster of cells, frequently with a smaller accessory group at one side, which lies beneath the nerve cord, partly in the second maxilla and partly in the first maxillipedal segment. Its position is marked externally by an inconspicuous swelling. The cells which compose this "gland" are arranged radially. There is apparently an indefinite central lumen but this shows no opening to the exterior. An opening may exist, however, as Claus ('84) figures an orifice in the similar structure which he describes for the young of an Adriatic Thalassinid, *Calliaxis*. The cells have a granular cytoplasm which does not stain deeply nor blacken on treatment with osmic acid; their nuclei are peripheral. As no distinct hypodermal cells can be seen in the region, the organ is probably a modification of the hypodermis. We have no clue to its function, although it somewhat resembles the glands with radially arranged cells which lie in the labrum and around the oesophagus of many Crustacean larvae. It seems as if this structure must rank with the asymmetrical mandibles as a distinction between the young of *Naushonia* and the young of most Decapoda.

ADOLESCENT DEVELOPMENT.

The lack of any approach to the adult form during the later pre-adolescent stages, together with the close resemblance that exists between adolescent and adult stages, makes the metamorphosis at the close of the mysis phase very striking. Moreover, the first adolescent is only six millimeters long, while the preceding stage

has a length of ten millimeters. No specimens of these stages occur at the surface, as the animal now is no longer a swimmer. I was able, however, to rear a few from the last preadolescent stage. These adolescent larvae were colorless, crawled actively on the bottom of the dish in which they were kept, darting away when disturbed, and though they concealed themselves in seaweed, they did not burrow in the sand supplied to them. They did not take animal food, at least while under observation, but collected and devoured considerable diatomaceous matter. In all movements the abdomen was extended and the chelipeds were held stiffly in front, the "thumbs" pointing inward and the "elbow" not flexed. The adult *Naushonia*, however, obviously carries the "elbow" slightly bent, the meros pressed against the carapace, the "thumbs" approximated, and the outer margins of the propodi separated. This difference between the adolescent and the adult recalls *Homarus*, where the first adolescent — fourth — stage keeps the "elbows" of its chelipeds straight, so that the apices are parallel, while the adult approximates the tips.

As can be seen by reference to the figures, these stages (pl. 2, fig. 27) closely resemble the adult shrimp, even the inevitable differences in the proportions of the parts being unusually small. The carapace has a broader external notch, larger rostrum, and stronger supra-antennal spine. Only cervical and longitudinal grooves are developed. The abdomen is a third shorter in proportion to the carapace but is otherwise like the abdomen of the adult. The telson (pl. 1, fig. 18) has a spine at the external angle. The eyes are visible from above. The flagella of the antennulæ and antennae are few-jointed, as is the rule among immature Decapoda. The antennal scale attains the base of the external spine, is smooth, and has the inner border finely, the outer coarsely serrate. The mandibles (pl. 2, fig. 28) are symmetrical and adult in form except that the palpus has an indistinct transverse division on the basal joint as if this latter represented two fused joints. The maxillae and maxillipeds (pl. 1, figs. 12, 13; pl. 3, fig. 42) resemble those of the adult, excepting the more deeply excavate base of the third maxilliped. The chelipeds (pl. 1, fig. 17) are symmetrical and slender, especially the outer joints. The length of the propodus is nearly four times the breadth, its occludent margin has three large and a number of smaller teeth, and, as in the adult, is half as long as the joint.

The propodi of the posterior pereopods are longer relatively to the whole limb than in the adult. The gills are as in the adult animal, but all the mastigobranchs, excepting the most anterior, are more slender, and the posterior podobranchs are small. The plates of the gills are linear or linear-oval. The pleopods are present on segments two to five and their rami are less lanceolate than in the adult (pl. 2, fig. 29). The uropods have narrower rami than in the adult and the transverse suture of the inner ramus is flexed. The material did not permit a study of the internal anatomy.

PROBABLE AFFINITIES OF NAUSHONIA.

The larvae of *Naushonia* find their nearest counterpart in those of another Thalassinid, *Calliaxis adriatica* (Heller). The young of this species have been described and figured by Cano ('91) and Claus ('84). Not only is their general form very much like that of the *Naushonia* young, but they also resemble them in all important anatomical details. The presence of a ventral gland with the same relations as in *Naushonia* is especially important in this connection. The mandibles also are similarly asymmetrical and have a similar relation to the sides of the body, the conical on the right, the arcuate on the left. The chief points of difference between the *Calliaxis* and the *Naushonia* larvae are found in the less arcuate rostrum of the Adriatic form which is not recurved at the tip; the relatively longer "neck" (if we may wholly credit Cano's figures, which seem rather crude, this equals the carapace in length in stage "A," exceeds it in "B," and is twice as long in "C"); the presence of hooks on the angles of the sixth as well as the anterior abdominal segments in the mysis stages (Cano); the more spatulate telson of the "mysis" which recalls the shape of the telson in larvae of *Gebia* (Sars, '84); the absence of a functional exopod on the fourth pereopods; the more rapid development of the green gland and the greater size of the ventral gland. None of these, however, are characters which detract from the essential likeness between the two forms.

The succession of the stages in *Calliaxis* is not clear. Cano apparently records five preadolescent stages, figuring the first ("A"), third ("B"), and fifth ("C," "mysis"). Of these, "A" corresponds

to my "first stage," and "B" to my "fourth stage" in *Naushonia*; "C" probably represents the last of the preadolescent stages, *i. e.*, is equivalent to my "fifth stage." Claus figures two early "stages" ("Länge von $3\frac{1}{2}$ mm.," and "aelteres Stadium"), which differ in size alone, and which correspond in the development of the appendages to my "first stage" and to Cano's "A." He also records two later stages ("Larven von $4\frac{1}{2}$ mm. Länge," "Larven von $7\frac{1}{2}$ mm. Länge") which are equivalent respectively to my "second" and "third" stages, but have no counterpart in Cano's series unless one of them corresponds to his "fase intermediaria tra A e B" of which no description is given. Claus makes no record of any stage equivalent to Cano's "B" and to my "fourth stage." In a later article ('85) he figures part of a "mysis," corresponding to my "fifth stage" and to Cano's "C." The series would then stand:—

Naushonia	(Claus)	(Cano)
I =	3.5 mm. + "aelteres"	= "A"
II =	4.5 mm.	"fase intermediaria tra
III =	7.5 mm.	A e B."
IV =		= "B"
		"fase intermediaria tra
		B e C."
V =	"mysis"	= "C"

If Cano is correct in his statement that there is a stage between "B" and "C," his and Claus' accounts can only be reconciled by supposing that the zoea-mysis period of *Calliaxis* comprises six stages.

Another Crustacean larva which somewhat resembles the young of *Calliaxis*, and hence those of *Naushonia*, has been recorded from the coast of England (Brook, '88), but unfortunately the description of this form is too imperfect for us to determine whether the similarities are more than superficial. Five stages were observed and it is stated that the "pereopods never pass through a schizopod stage." The parent of this larva is not known.

Outside of the young of *Calliaxis*, however, and possibly also of this "trachelifer," no other Decapod larvae have been described that even remotely resemble those of *Naushonia* in form or structure,

and among those Thalassinidea in which the development has been studied the immature stages are not at all similar; viz., *Axius* (Cano, '91); *Gebia* (Cano, '91; Sars, '84); *Callianassa* (Cano, '91; Claus, '76); *Calocaris* (Sars, '84).

The question then arises whether the possession of so unusual a common structure in the *Calliaxis* and *Naushonia* young is significant either as the result of a convergence perhaps due to some manner of life, or as indicating actual relationship between the parents.

On the whole, ontogenetic stages among the Crustacea are very properly regarded as unsafe guides to relationship. Not only is there that strong tendency toward palingenetic structure throughout the class, which has given us the zoea and probably also the nauplius, but further, larvae belonging to closely allied species, as for example, those of *Lucifer* and *Sergestes*, or the young of brackish or fresh-water forms as compared with their marine congeners, are frequently very dissimilar in appearance. But it must not be forgotten on the other hand, that the zoea and nauplius frequently serve as valuable criteria for relationship in the groups in which they occur, and the immature stages of species belonging to allied orders or families often possess common structural characters which may, moreover, be to a greater or less degree distinctive for the group or groups in question. The abdominal armature of Caridean zoeae, the shape of the eyes and telson in the majority of Thalassinoid and Paguroid larvae, and the peculiar zoea of the Brachyura are illustrations of this. A more striking instance still is the "phyllosoma" larva characteristic of the Loricata.

Usually also when differences separate the young of related species, these are found on closer examination merely to mask a more or less fundamental likeness. But the peculiar structures which unite the young of *Naushonia* and *Calliaxis*, while separating them from the larvae of other Thalassinids, seem to be deep-seated. The asymmetry of the mandibles in the zoea and mysis stages is, so far as I can determine, unique among Malacostracan larvae at least. Typically, the zoea is symmetrical in all points, whatever the condition of the adult, and the final asymmetry enters during the later development. The ventral gland is also a very unusual structure. Claus ('84), indeed, hints at the presence of an homologous "Auf-treibung zwischen den Maxillen und vorderen Kieferfusspaar" in

Pagurid zoeae, but I have not been able to find a trace of such a structure in the genus *Eupagurus*.

In the face of the foregoing considerations, it certainly seems much more likely that the common structure of the young of *Calliaxis* and *Naushonia* is to be explained as due to relationship between their parents, rather than as a result of independent development in each species. The only direct evidence in favor of the latter view is the isolation of the two genera geographically. The zoea and mysis stages of *Naushonia* offer no peculiarity in their mode of life.

The supposition of relationship of course makes no attempt to explain the origin of the unusual anatomical characters of the larvae, which is completely obscure. It merely assumes that they were received in both species as a legacy from common ancestors, in which they arose as an adaptation to a peculiar need, or perhaps merely as a variation which was not injurious and became prepotent, undisturbed by selective processes. In either event the alterations when once fixed, might readily be handed down even if in the descendants they were without selective significance. The supposition is also in perfect accord with the result obtained from comparison of the parent forms. I am unable to give a description of *Calliaxis* at first hand, since the species is rare and specimens could not be obtained. But the animal and many of its appendages were described with considerable detail by its discoverer, Heller ('62), and these data are amplified and supplemented by the briefer accounts in the writings of Cano ('91) and Claus ('85).

Comparison of these descriptions and figures with *Naushonia* shows an essential likeness between both species in almost all anatomical details, especially with respect to the carapace, abdomen, gills, and posterior mouth parts. Only the pereopods and the appendages of the head are to any extent dissimilar. The carapace lacks the keels and supra-antennal spines and the external notch is weaker than in *Naushonia*. The triangular, serrate rostrum has a slight median furrow. The abdomen differs in the more acutely rounded epimera, which are, however, procurvent, recurrent, or truncate, respectively, as in *Naushonia*, and in having the surface of the telson marked by a median furrow and two lateral keels. The gill formula is identical in both genera and the structure and relative proportions of the slightly phyllobranchiate gills are the same, except that the European genus has the anterior gill on segment 4 smaller than its fellow, the mastigobranchs narrow and weak, espe-

cially those on the pereopod segments, and "calcified bars" are absent from their bases. Only males have been collected, and these bear pleopods on the second to the sixth abdominal segments. The rami of these pleopods are less acutely pointed than those of *Naushonia*'s pleopods. Heller clearly figures these appendages without a stylamblys (pl. 3, fig. 50), so that Cano's assertion that this appendix is present has little weight. The uropods have broad-oval rami and the transverse suture on both is flexed. The surface of the outer ramus is traversed by one, the inner by two longitudinal keels.

As already noted, the posterior mouth parts are of the same type in both genera, *Calliaxis* showing those peculiar modifications of the maxillae (pl. 3, figs. 44, 46) and maxillipeds (pl. 3, fig. 47-49) which are distinctive of *Naushonia*. The relative proportions of the parts of each appendage are also quite similar, with the following exceptions: the first maxillae have a more acute internal lacinia and a shorter palpus than in *Naushonia*; the second maxillae have those divisions of the external and internal laciniae which are adjacent to one another, narrower than the outer divisions of these laciniae, while in the American genus all the divisions are more nearly sub-equal; the scaphognathite is narrower; the expansion of the "endopod" in the first maxilliped is spatulate rather than triangular and the flagellum of the exopod is shorter; the flagellum in the exopod of the second maxilliped is not as long as the peduncle; and in the third maxilliped the area of stiff bristles on the fourth joint is replaced by a serrate keel. Heller and Cano do not agree as to the length of the peduncle of the exopod in the second maxilliped, the former figuring it as equaling the endopod, the latter as only reaching the middle of its fourth joint.

The first peduncular joint of *Calliaxis*' antennula is short and the third elongate, while in *Naushonia* these joints are "long" and "moderate" respectively. The antennae have an elongate peduncle which exceeds the flagellum of the antennulae; the first, second, third, and fifth joints are short, the fourth is elongate. The first joint bears three teeth on its distal border, the second has a blunt external spine. The flagellum is long and slender and the scale is reduced to a "flat, three-cornered spur (stachel)."¹

¹ Cano asserts that this is absent, but his description and figures seem unreliable.

The eye-stalks in *Calliaxis* are slightly flattened and are proportionally longer than in *Naushonia*. The anterior pereopods (chelipeds) are very large with a long, slender dactylus and are perfectly chelate. The shape and proportions of the posterior pereopods are more as in *Naushonia*. According to Heller's descriptions, the second and fifth pairs are slightly subchelate, but Cano describes them as simple.

The form of the mandibles cannot be definitely deduced from descriptions or figures (pl. 3, figs. 43, 45). If the blade is not excavate, which is a possible interpretation, we have here an important difference from *Naushonia*. Its border is without teeth. The mandibular palp is proportionally rather long, three-jointed, and the apical joint is densely hairy.

From the foregoing comparison of the adults, we can scarcely doubt that *Naushonia* and *Calliaxis* are allied genera, although occurring in widely separated localities. They must then be considered together in any systematic arrangement of the Thalassinoid Crustacea, and data derived from knowledge of one will be valuable in indicating the affinities of the other. Unfortunately the same uncertainty that has already been noted with respect to *Naushonia* holds good for *Calliaxis* also. Its position has always offered difficulties to systematists, and with the exception of Heller, in 1862, and Bate ('88) and Ortmann ('98) in more recent years, carcinologists have avoided a definite expression of opinion. These authors also place the genus more or less tentatively, and their assignments are diverse. Heller makes it part of his "family" *Thalassinidae*, a group with the rank and almost the same scope as the modern "division" *Thalassinidea*, and suggests that it comes near de Haan's genus *Laomedea*. This latter genus, however, is only imperfectly known, so that the correctness of this conclusion cannot be properly tested, and even if confirmed, would be of little assistance. Bate ('88) groups *Calliaxis*, *Calocaris*, and *Thaumastocheles* in one family, *Thaumastochelidae*, which he places in his *Macrura aberrantia*, i. e., nearer to the *Thalassinids* than to the *Nephropsidea*, which form part of his *Macrura normalia*. He does not mention the genus *Laomedea*. The reasons for this union of *Calocaris* with *Thaumastocheles*, however, are not at all apparent, and although *Calliaxis* resembles the latter genus in the structure of its antennae, maxillae, and second maxillipeds, it does not seem to lie very close to it.

Thaumastocheles is rather Nephropsidean in its characters. Both *Calocaris* and *Calliaxis*, on the other hand, are more Thalassinoid, and Ortmann ('98) recently has separated the genera, placing *Thaumastocheles* in the Nephropsidea, *Calliaxis* and *Calocaris* together with *Laomedia* in the family *Axiidae* of the Thalassinidea. This classification is in perfect accord with the Axiid affinities of *Calliaxis*' ally, *Naushonia*. And although it must not be regarded as at all final, it may well be accepted as more natural than any other arrangement which is possible at present.

There is great need, however, for a thorough revision of the Thalassinoid Crustacea, and until that is made, the relations of the genera to one another must remain obscure and any separation into families be more or less tentative. Ortmann distinctly states this in connection with the systematic arrangement just cited ('98, p. 1141). Such a welcome aid to research, however, cannot be attempted as yet. It must await a more ample knowledge of the anatomy of the individual forms, and all study should hold that end in view. The present article, then, only attempts to give an account of two of the more imperfectly known genera of the Thalassinidea and of the remarkable character of their larvae. Of these, *Calliaxis* is probably to be regarded as the more specialized since it has a reduced antennal scale, small mastigobranchs, weaker epimera, and more perfectly formed chelicipeds. In its development, also, its larvae present the strange form to a greater degree than do those of *Naushonia*; the metamorphosis is slightly more concentrated, the fourth pereopods never having functional exopods; and the peculiar ventral gland is larger.

The establishment of the true position of these genera within the Thalassinidea must be left to future students. But it seems probable that research will tend to intensify rather than to diminish the differences that separate them from other members of the group. *Calliaxis* and *Naushonia* may be regarded as aberrant forms, probably from pre-Axiid stock, which have retained characters that ally them on the one hand to the more primitive *Axiidae* and on the other suggest relationship with genera of the Nephropsidea. And their evolution has been along lines apart from that of most Thalassinids, especially in the development of the very unusual larval form.

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(Development of *Calocaris macandreae* and *Gebia littoralis*.)

Printed, March, 1903.

PLATE 1.

(All figures are from camera lucida drawings by the author unless otherwise noted.)

- Fig. 1. Adult *Naushonia*, female specimen; right side. $\times 4.5$. pr₂, second pereopod; t, telson; abd₂, second abdominal segment; sl, longitudinal groove; a₁, antennula; a₂, antenna.
- Fig. 2. Head of male specimen; left side. $\times 70$ (?). sor, supra-orbital keel; ex, scaphocerite of antenna.
- Fig. 3. Tail-fan. $\times 6$.
- Fig. 4. Head of male specimen; dorsal side. $\times 23$. ex, scaphocerite; sor, supra-orbital ridge; sc, cervical groove; sl, longitudinal groove.
- Fig. 5. Third maxilliped; basal portion, inner face. $\times 20$.
- Fig. 6. Mandible; inner face. $\times 16$ (?).
- Fig. 7. First maxilla; ventral side. $\times 16$ (?). li, lacinia interna; p', palpus.
- Fig. 8. Second maxilla; ventral side. sc, scaphognathite; en, endopod; le, lacinia externa; li, lacinia interna.
- Fig. 9. Second maxilliped; ventral side. $\times 27$. mb, mastigobranch; pb, podobranch; en, endopod.
- Fig. 10. First maxilliped; mastigobranch removed. $\times 12.5$. en, endopod.
- Fig. 11. Second pereopod; distal portion.
- Fig. 12. First maxilliped; adolescent, ventral side. $\times 23.5$. en, endopod; ex, exopod.
- Fig. 13. Apex of endopod, second maxilliped; adolescent.
- Fig. 14. Mastigo- and podobranch of third maxilliped; adult.
- Fig. 15. Mastigo- and podobranch of second pereopod of adult. cb, calcified bar.
- Fig. 16. Mastigobranch of fourth pereopod of adult. ab, arthrobranchs of same segment.
- Fig. 17. Chela of more advanced adolescent stage.
- Fig. 18. Tail-fan; adolescent. $\times 6$.
- Fig. 19. Second pleopod; adult, anterior surface. $\times 12$. ir, inner ramus.

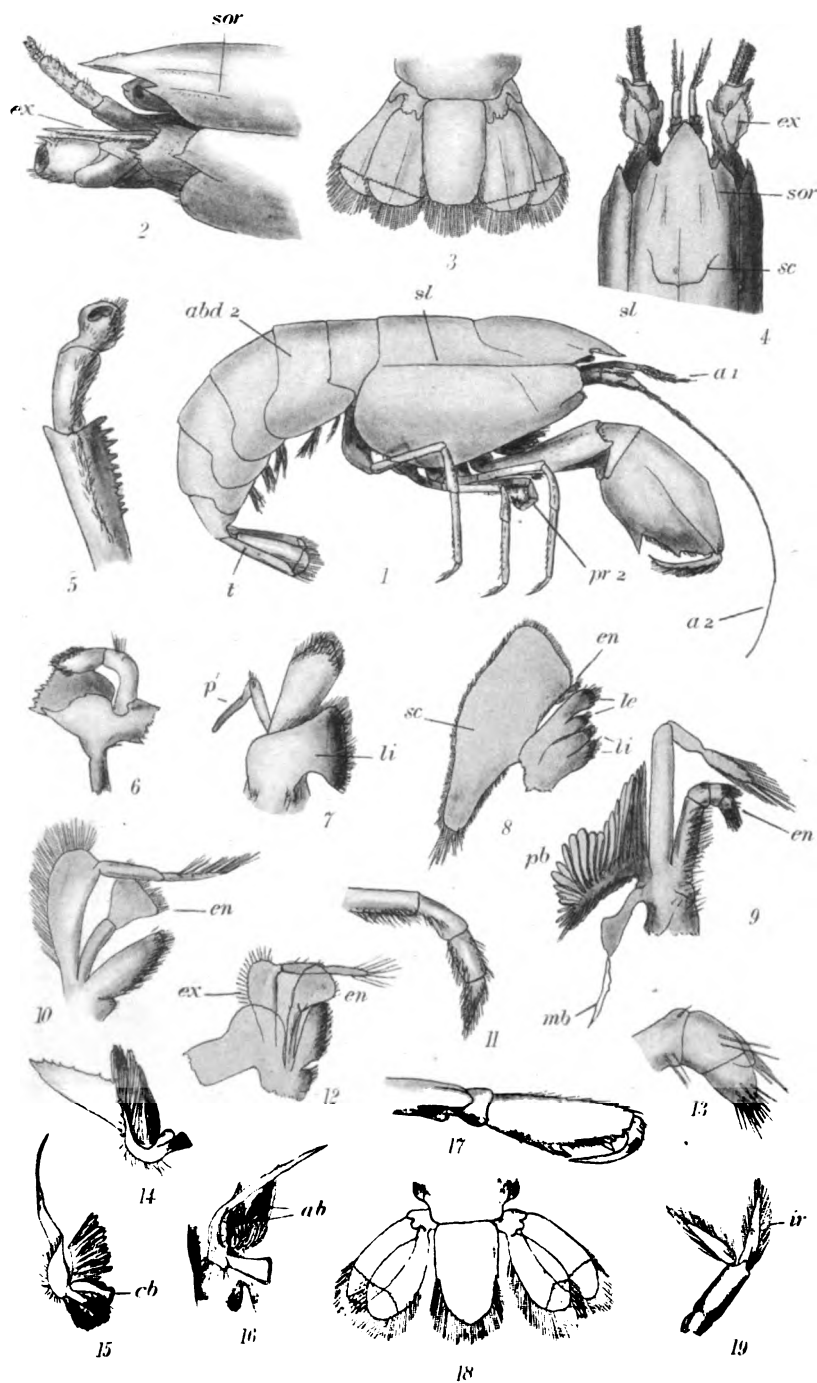
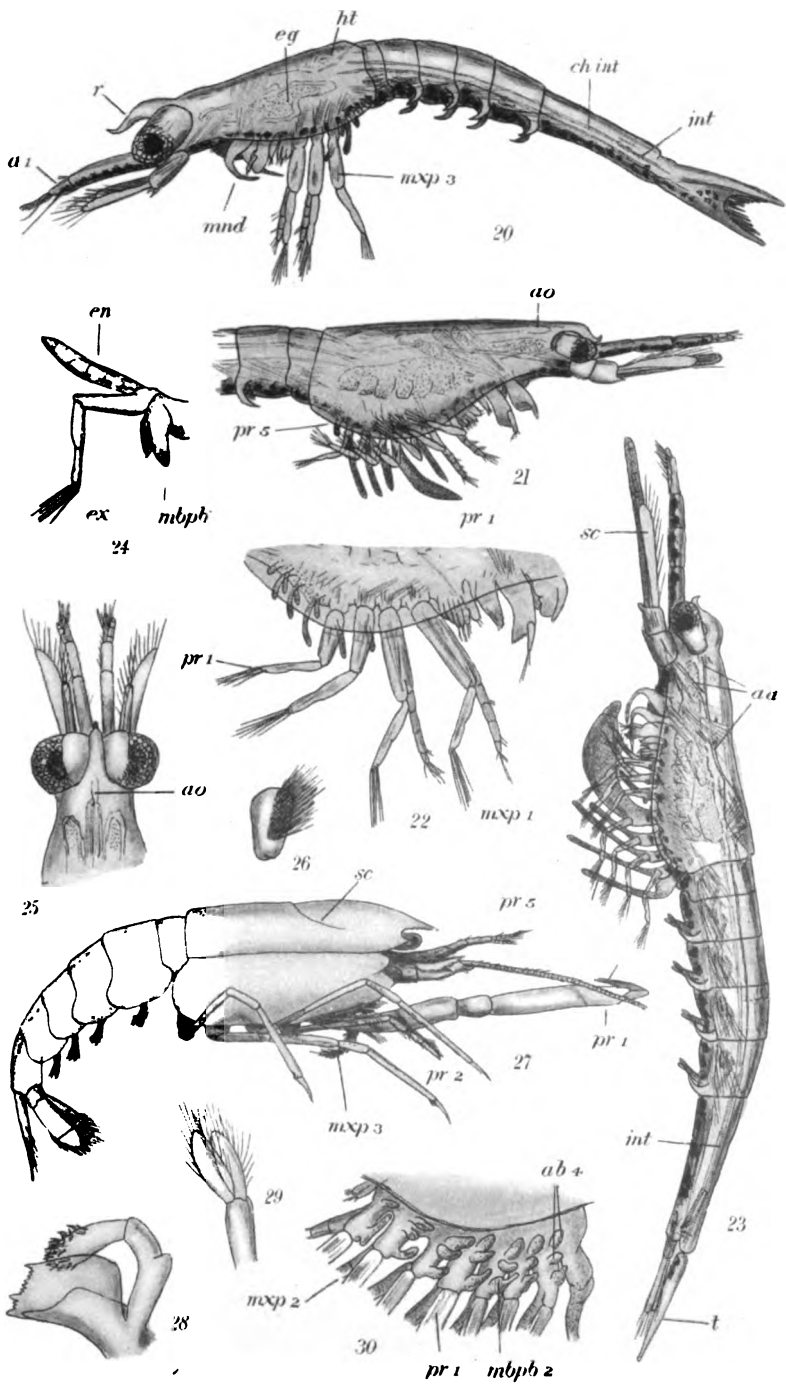


PLATE 2.

- Fig. 20. Second larval stage; left side. $\times 37$. mxp₃, third maxilliped; mnd, mandible; eg, liver; ht, heart; ch int, chitinous gut; int, achitinous gut; r, rostrum; a₁, antennula.
- Fig. 21. Thorax of fourth stage; right side. $\times 30$. pr₁, first pereopod; pr₅, fifth pereopod; ao, aorta.
- Fig. 22. Thorax of third stage; right side. $\times 30$. pr₁, first pereopod; mxp₁, first maxilliped.
- Fig. 23. Fifth stage; left side. $\times 20$ (?). pr₅, fifth pereopod; sc, scaphocerite of antenna; int, achitinous gut; aa, antennary artery; t, telson.
- Fig. 24. Third maxilliped, fifth stage. mbpb, mastigo-podobranch rudiment; ex, exopod; en, endopod.
- Fig. 25. Head of fourth stage; dorsal side. $\times 26$. ao, aorta.¹
- Fig. 26. Fourth joint of third maxilliped; adult.
- Fig. 27. First adolescent stage; right side, showing manner of carrying cheliped. $\times 70$. pr₁, cheliped; pr₂, second pereopod; mxp₃, third maxilliped; sc, cervical groove.
- Fig. 28. Mandible of adolescent; ventral side. $\times 42$ (?).
- Fig. 29. Pleopod of adolescent. $\times 20$.
- Fig. 30. Gill rudiments of fifth stage. mxp₂, second maxilliped; pr₁, cheliped; ab₄, arthrobranchs of fourth pereopod; mbpb₂, common rudiment of mastigo-podobranch of second pereopod.

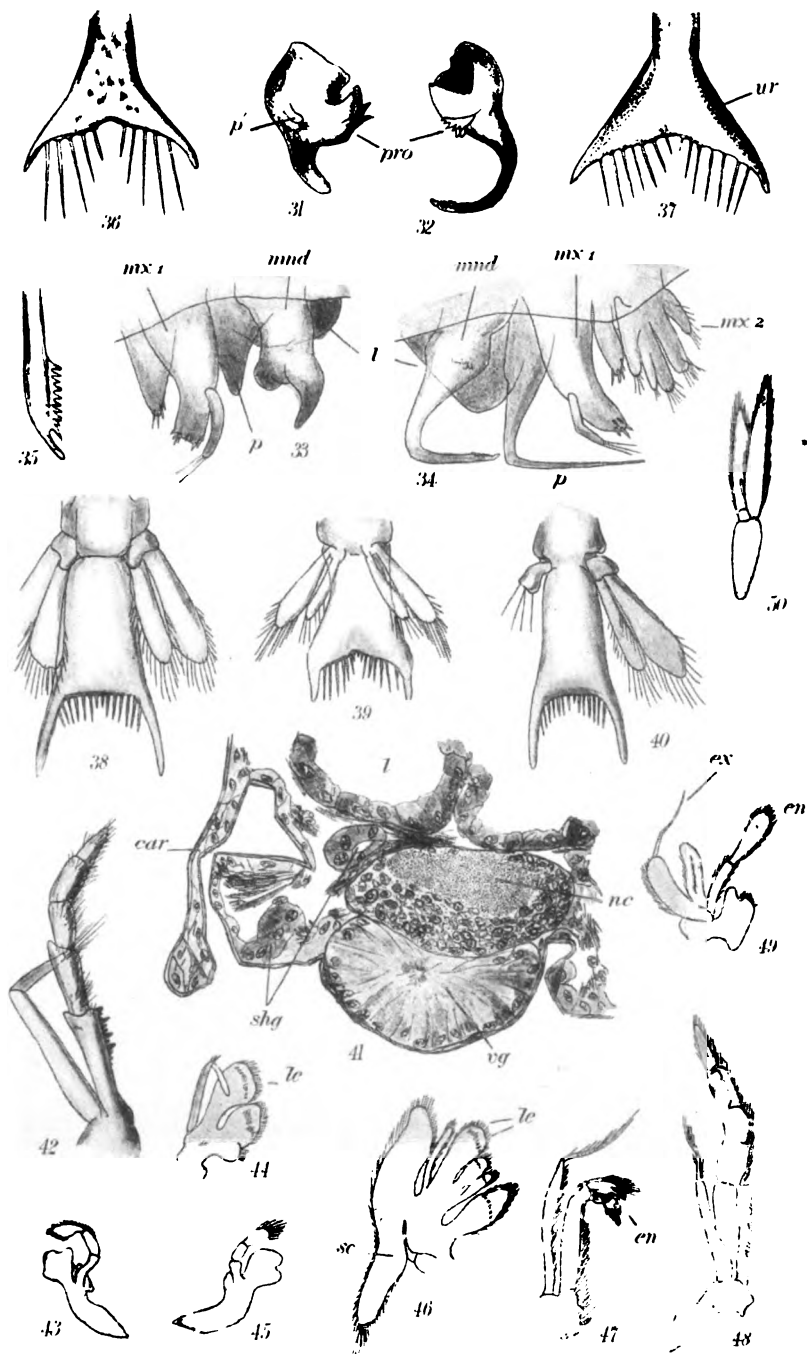
¹The endopod of the antenna is incorrectly drawn; it should be naked and longer than the exopod.



Not Thompson's.

PLATE 3.

- Fig. 31. Right mandible; fifth stage, inner face. pro, process; p', palpus.
 Fig. 32. Left mandible; same. pro, plate and crest equivalent to process on right mandible.
 Fig. 33. Mouth parts of same; right side. mnd, mandible; l, labrum; p, paragnath; mx₁, maxilla.
 Fig. 34. Same; left side. Letters as before.
 Fig. 35. Apex of left mandible of same; more enlarged.
 Fig. 36. Telson; first stage, ventral side.
 Fig. 37. Same; second stage, dorsal side. ur, anlage of uropod.
 Fig. 38. Tail-fan of fifth stage; dorsal side.
 Fig. 39. Same of third stage; ventral side.
 Fig. 40. Same; fourth stage ventral side.
 Fig. 41. Ventral gland, first stage; transverse section through second maxilla. $\times 195$. car, carapace; shg, shell gland; l, liver; nc, nerve cord; vg, ventral gland.
 Fig. 42. Third maxilliped; adolescent, ventral. $\times 20$ (?).
 (Figures 43–50 are outlines of the appendages of *Calliaxis adriatica* drawn from Heller's and Cano's figures.)
 Fig. 43. Mandible (Heller).
 Fig. 44. First maxilla (Heller). le, lacinia externa.
 Fig. 45. Mandible (Cano).
 Fig. 46. Second maxilla (Heller). le, lacinia externa; sc, scaphognathite.
 Fig. 47. Second maxilliped (Heller). en, endopod.
 Fig. 48. Third maxilliped (Heller).
 Fig. 49. First maxilliped (Heller). en, endopod; ex, exopod.
 Fig. 50. Pleopod (Heller).



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